7 Allocation of resources. nutrient uptake and release by decomposer organisms.

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Introduction

The activities of decomposer organisms are thought to be a major pathway by which mineral nutrients elaborated into plant and animal material are returned to the soil/root system available for uptake by plants. During decomposition a large proportion of the plant carbohydrate is lost as carbon dioxide by microbial respiration.

The composition of the initial substrate has a profound effect on the type of colonization (Hudson 1968). Particular attention has been paid to carbohydrate status (Garrett 1962, Merrill & Cowling 1966). Garrett (1956) and Hudson (1968) both emphasize that colonization of plant parts begins long before they die. Early colonists must either be parasitic or 'commensal' to obtain sufficient carbohydrate and mineral nutrients. The 'commensal' phylloplane/rhizosphere floras depend on materials diffusing in solution, as do the balanced biotrophic parasites. The latter group have much more exacting nutrient requirements than the epiphytic organisms, if behaviour on artificial media forms an adequate basis for judgement. Two groups of colonists of dead plant material are thought to depend largely on 'soluble substrates'—primary and secondary sugar saprophytes. The remainder are capable of utilizing complex carbohydrates and as such are responsible for the disposal of the bulk of plant debris.

The study of nutrient requirements of those organisms, normally dependant on soluble sources of nutrient, on liquid or semi-solid media is a reasonable model of the natural situation. This is not the case with organisms which normally depend largely on cellulose, lignin or other complex substances. The behaviour of these organisms in a medium composed of soluble, evenly distributed, and diffusible nutrients may well be different from that on natural substrates.

There are further limitations to the applicability of results from liquid/agar cultures to the situation in plant litter or soil. The most important is the spatial concentration of each nutrient. Even if the concentration of the liquid medium is adjusted to the average, say, of wood (Park, Chapter 3), there is no way of producing local pockets of nutrients such as are found in medullary ray cells. Such local concentrations may well allow organisms to grow in habitats in which the *average* concentration of nutrients would be insufficient. The spatial localization in faecal pellets is discussed by Hissett & Gray, Chapter 2, and Hargrave, Chapter 13 (this volume), in soil and aquatic systems respectively.

The following account deals first with the natural substrate, and with the changes in nutrient amounts and concentration observed during decay. The second part deals with the behaviour of selected organisms in pure culture with regard to allocation of nutrients during growth in and 'decay' of artificial substrate. The gulf between the two is in part due to the basic differences in substrate type outlined above. In part it is due to the lack of widely accepted methods for separating microbial components from substrate components in opaque and physically heterogeneous media.

The substrate

Plant materials contain a variety of mineral nutrient sources. Nitrogen is mainly in protein form either as protoplasts or in the cell walls. After cell death it is usually bound up with oxidized polyphenols (Wood 1964). Smaller amounts of nitrogen are found in nucleic acids, membrane lipo-proteins, amino-sugars and lignin. During decay increasing amounts become incorporated into microbial protein, and into amino-polysaccharide cell walls.

All forms of nitrogen have to be digested by enzymes before they are available to saprophytic micro-organisms.

Phosphorus is present in membrane phospholipid, in nucleic acids, and as polyphosphates, particularly of inositol (phytic acid). Very little is present as inorganic phosphate (P_i) ion. All the organic forms (P_o) have to be degraded before assimilation.

Potassium and calcium contrast with N and P, in that both are mostly present as simple inorganic ions in the living plant. Potassium (K^+) is present in cell vacuoles, and calcium as insoluble calcium pectate in cell walls. A large proportion of the nutrients, particularly phosphorus, present in the live leaf may be back translocated (Rodin & Basilevitch 1967) before death to overwintering rhizomes or roots. The residue fraction in the leaf is unlikely to be readily available to micro-organisms.

The nutrients present at death will be competed for by micro-organisms, but soluble ionic forms will also be depleted by leaching. This type of loss must affect soluble ionic nutrients much more than those in insoluble or organic forms. At present it has not been quantified and, indeed, is extremely difficult to assess, since the amount of leaching will vary with both intensity and duration of rainfall as well as with the rate of drying and the nature and position of the materials subjected to leaching.

MOBILIZATION OF MINERAL NUTRIENTS

The nutrients sequestered by micro-organisms will at first be indistinguishable from substrate nutrients in total analyses (Fig. 7.1). However, microbial activity is accompanied by respiratory loss of carbon as CO_2 and often consequent narrowing of carbon/nutrient ratios (Table 7.1). When nutrients sequestered are translocated outside the substrate via hyphae (e.g. mycorrhizal fungi) or by mycelial aggregations, or to fruiting structures on the surface, then the carbon/nutrient ratio will widen (Table 7.1). It is because these ratios are the resultant of two independent processes that they are un-

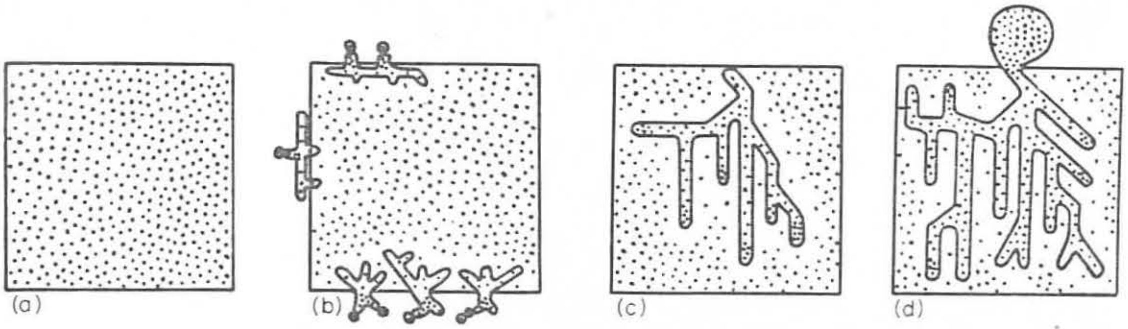

Figure 7.1. Changes in nutrient location with time in decomposing substrates.
(a) Original, uncolonized substrate with nutrient units as dots.
(b) Extraction of nutrients near surface only by rapidly sporulating surface colonists.
(c) Colonization by pervasive fungus with nutrient absorption by hyphae, but no overall change.
(d) Mobilization by pervasive fungus to massive exterior fruit body, with resultant drop in nutrient concentration in substrate.

Table 7.1. Changes in Carbon/Nitrogen and Carbon/Phosphorus ratios with time in leaves of *Eriophorum* spp. at Barrow, Alaska and Moor House, U.K., and soil ratios at the same sites.

Year		0	1	2	3	4	soil
E. angustifolium	C/N	17·2	29·4	42	42		21
(Barrow)	C/P	500	417	454	999		5,520
E. vaginatum	C/N	50	42	33	28	25	53
(Moor House)	C/P	877	767	635	556	504	450

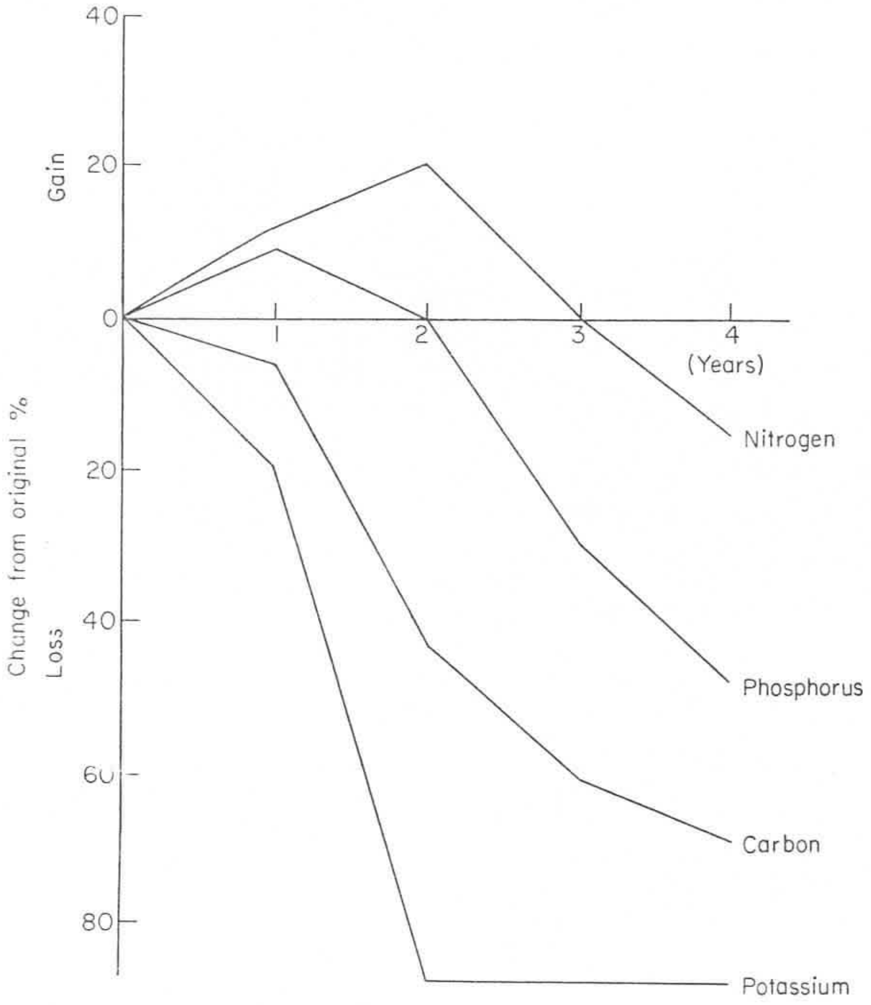

Figure 7.2. Changes in amounts of C, N, P and K in decaying leaves of *Rubus chamaemorus* at Moor House, U.K. expressed as a % of original amount present (after Dowding 1974).

satisfactory and conceal very different rates of nutrient loss (Fig. 7.2). The observation (Hawker 1951, Cochrane 1958) that changes in substrate C/N ratio *cause* fruiting in certain fungi is also open to criticism, in that the observed change in ratio may well be the *effect* of mobilization of protoplasm and stored nutrients to the (external) fruiting site.

Gotz *et al.* (1973) observed that in a mixed hardwood forest losses of nitrogen exceeded carbon losses when initial litter C/N ratios were below 20–30 ('critical point') and that litter C/nutrient ratios tended to stabilize near those of the underlying A horizon. The 'critical point' appears to be site specific but is not directly related to soil/nutrient ratio (Table 7.1) at Tundra IBP sites. Such equilibration of *ratios* is a result of so many different factors that its use creates more problems than it solves.

It has frequently been observed (e.g. Kendrick & Burges 1962) that the comminution phase of decomposition is delayed until some fraction of dry weight has been lost by microbial respiration. Increased digestibility is thought to be caused by higher nutrient concentrations, or to microbial metabolism of toxic or indigestible compounds. A coincident change in physical environment (the overlying layer of fresh litter) which allowed greater microfaunal activity could also be the cause.

Another effect of micro-organisms, that of concentrating the mineral nutrients from a relatively large volume of indigestible material into a digestible form (as spores/fruit bodies), has been noted by Leach (1940), Franke-Grossmann (1963) and Dowding (1973) among others. The destruction of hymenomycete fruit bodies by slugs and dipteran larvae is an example of the same phenomenon. In addition to concentrating the nutrients and presenting them in a more palatable form to saprovores, micro-organisms may also synthesize growth factors (Baumberger 1935; Leach 1940, Dowding 1967). This is certainly one of the advantages of the gut flora to the ruminant (Weller *et al.* 1958). Most spores that are not consumed before they are dispersed do not land on suitable host or substrate, and are washed out or fall out of the air on to the soil. They are there consumed by animals or other micro-organisms, so contributing to the biological cycle of nutrients.

Pure culture studies

Nutritional studies in pure culture have been largely conducted with liquid media (Burnett 1969; Cochrane 1958). The system has a number of advantages when compared with natural substrates (Table 7.2) but, with the exception of commensal organisms is one rarely met with in nature. Hybrids, such as cellulose in mineral solution (e.g. Chang & Hudson 1967; Bhargava 1972) are frequently used, but suffer particularly from the inseparability of substrate and micro-organism. Another disadvantage shared by most artificial media, is their insufficiency as far as Basidiomycete fruiting is concerned.

Table 7.2. A comparison of the attributes of liquid and natural solid media.

	Liquid	Solid
Spatially uniform	✓	
Separable from micro-organism	✓	
Definable	✓	
Substrate loss quantifiable	✓	✓
Sporing structures separable		✓
Sporing of higher fungi		✓

YEASTS

Some of the earliest organisms investigated were yeasts (Prescott & Dunn 1959), both as sources of protein and of fat (Fig. 7.3), where either carbohydrates or nitrogen (as protein) were stored by the yeast cells if they were in excess of the other. Large amounts of nitrogen caused much greater utilization of the P and K in the medium than when nitrogen was limiting (Table 7.3). Yeast cells appeared to be able to modify nutrient ratios (Table 7.3), primarily by accumulation of mobilizable carbohydrate. Phosphorus and potassium were 'spread' more thinly when they were limiting growth (Table 7.3).

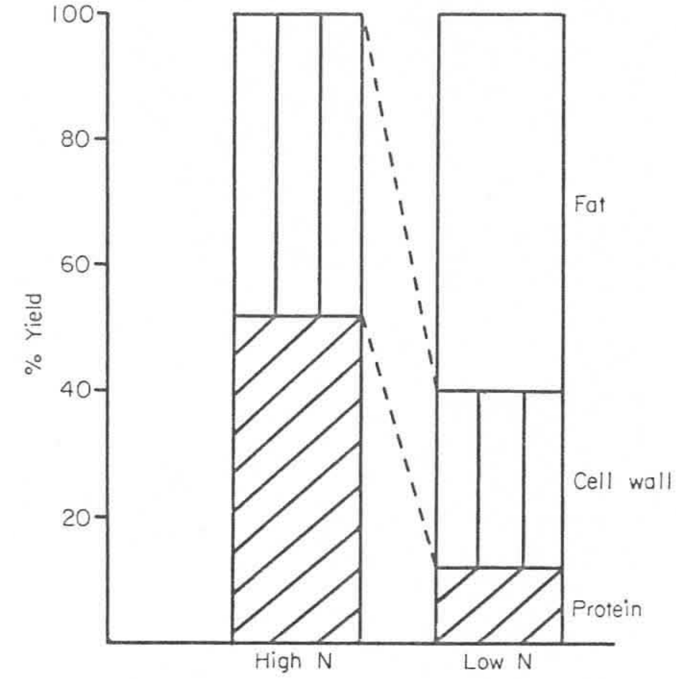

Figure 7.3. Crude fractions of yeast dry weight in protein, fat, and cell wall on media at two levels of nitrogen (after Prescott & Dunn 1959).

Table 7.3. Percent of nutrients in media taken up by yeast cells, and the final carbon/nutrient ratios of the cells, under two nitrogen regimes.

Nutrient	N	P	K
High nitrogen 73 g l^{-1}			
Percent uptake	66	100	100
Cell carbon/nutrient	6	26	24
Low nitrogen 10 g l^{-1}			
Percent uptake	45	53	25
Cell carbon/nutrient	25	56	48
Cell carbon/nutrient (if fat removed)	6	14	12

MYCELIAL FUNGI

Various forms of mycelial fungi have been investigated, and a network of tubes within which protoplasts could move freely would seem an ideal means of allocating scarce nutrient resources first to exploitation of the substrate, then to reproduction (Burnett 1969).

Among the fungi imperfecti, *Botrytis cinerea* Pers. Ex. Fr. was shown to produce sclerotia when nitrogen was limiting and conidia when N was freely available (Pieris 1947). The form of nitrogen was not important (Leach & Moore 1966). Sclerotial formation would appear to demand excess carbohydrate as it was not observed under limiting N conditions by Dowding & Royle (1971). They found that under low N (C/N=250) (Table 7.4) most of the nitrogen was assimilated in the first three days, but under high N assimilation was more gradual and was reduced if P was limiting. Phosphate uptake was far less efficient, but under limiting conditions little more was taken up by cultures over three days old. Phosphorus uptake was limited by low N levels. When either N or P was limiting the mycelium continued to assimilate carbon, though at a lower rate than non-limited cultures (Table 7.5). The carbon/nutrient ratios attained are strikingly higher for *Botrytis* than for yeast cells (Tables 7.3 and 7.5).

Table 7.4. Percent of nutrients in medium taken up by *Botrytis cinerea* after 3 and 14 days (amounts in mg/flask).

Nutrient regime		N		P	
		3 days	14 days	3 days	14 days
Low N (1 mg)	High P (2·5 mg)	80%	80%	2%	5%
High N (10 mg)	Low P (0·25 mg)	7%	30%	10%	11%
High N (10 mg)	High P (0·25 mg)	8%	80%	2%	70%

Table 7.5. Final (14-day-old cultures) carbon/nutrient ratios of *Botrytis cinerea* mycelia. (Nutrient regimes as in Table 7.4.)

Nutrient régime		C/N	C/P
High N	High P	20	200
High N	Low P	50	5,000
Low N	High P	170	1,750
Low N	Low P	160	5,100

Chalal & Gray (1968) grew a number of fungi on wood pulp amended with soluble nutrients, and measured nitrogen immobilization after five days' growth. *Myrothecium verrucosum* and *Rhizoctonia solani* took up 60% of the available N and *Polystictus versicolor*, *Chaetomium globosum* and a number of Fungi Imperfecti 40–50%. The amount of dry matter in the fungi was not determined. The net weight loss only gives an estimate of growth, assuming a metabolic efficiency of 50% (Burnett 1969) (Table 7.6). The estimated C/N ratios are low compared with Levi and Cowling's (1968) for *Polystictus versicolor* of 73–278. The variation recorded by these authors is ascribed to adaption to extremely low substrate nitrogen. The age of the colony also has a great effect (Levi & Cowling 1969; Dowding & Royle 1971).

Table 7.6. Weight loss of wood pulp (orig. 750 mg) after 5 days' decay by various fungi, estimated weight of fungus (assuming carbon assimilated = 50% carbon absorbed), and weight of nitrogen immobilized.

Fungus	Weight Loss (mg)	Estimated fungal mycelium (mg)	Nitrogen (mg)	C/N /(fungal)
Trichoderma sp.	298	150	8·6	27
Chaetomium sp.	190	95	10	9·5
Polystictus versicolor	260	130	8·6	15

The commercial mushroom has also been studied by Treschow (1944) and Watson (1974). Watson (1974) found that mycelium in defined liquid culture could vary its N and P content adaptively (Table 7.7). Efficiency of phosphorus uptake was much lower than for nitrogen uptake (Table 7.7) and nitrogen uptake was more affected by limiting P than vice versa. Most of the phosphate uptake occurred early with the exception of cultures given organic phosphates as a phosphorus source.

Table 7.7. Carbon/nutrient ratios of 6-week-old *Agaricus bisporus* cultures on liquid media (n = 3), and efficiency of uptake from the medium.

		Mycelial ratio		Uptake efficiency/%	
	Medium ratio	C/N	C/P	N	P
Not limiting	C/N 20–100 C/P 50–200	15	541	31	2·2
P—limited	(C/P 400)	60	250	1	6·0
N—limited	(C/N 200)	40	417	37	1·0

Experiments on mycelial cultures as food (Prescott & Dunn 1959) gave mycelia with C/N ratios of 60 and C/P ratios of 40 after a short growth period.

During the vegetative phase some of the nitrogen assimilated by the micro-organism has to be re-exported as enzymes, particularly if insoluble carbohydrates forming the carbon source. Levi & Cowling (1968) found that cellulase production by *P. versicolor* was reduced at low N concentrations, but not proportionately. They also found that there was accumulation of fat under these conditions (cf. yeast cells) and that almost all the available nitrogen had been taken up after 14 days' growth. The relative proportion of nitrogen in nucleic acids increased with decreased nitrogen concentration until 25% of nitrogen assimilated in nucleic acids at medium C/N ratios $\geqslant 1{,}600$.

ALLOCATION TO REPRODUCTION

The degree to which reproduction, or sporophore and spore production, acts as a drain on the mycelium increases with the complexity of the fruiting structures. This hypothesis has been used to explain the succession of fruit bodies on herbivore dung (Webster 1970) but does not explain succession on other substrates, except perhaps on wood (Chesters 1950). Even if the mycelium of fungi can adapt its N and P content to the exigencies of the medium it is unlikely that spore nutrient content can vary as widely. It would be far more plausible to adopt Salisbury's (1942) hypothesis, that for any species the size and content of sexually reproductive propagules are largely genetically fixed, and that the only adaptation possible in starvation conditions is to reduce the number produced by each individual. Even though they are asexual propagules, the majority of conidia would fall into this principle, since their size is constant enough for taxonomic purposes.

The nutrient content of spores is always high. Merill & Cowling (1966) report spore C/N ratios of 12 for *Fomes pinicola* growing on wood with C/N ratios >400. The C/N ratio of the fruit body was 50. C/N ratios for mushroom fruit bodies are reported as 8 (Prescott & Dunn 1955 and Watson 1974). Merill & Cowling (1966) estimated that to provide the nitrogen in the fruit body and in the spores produced each year, *F. pinicola* would need to extract *all* the nitrogen from 0·2 cubic metres of wood. Such total extraction is probably impossible, if only because some N will be left in hyphal walls.

Both *Agaricus bisporus* on compost (Watson 1974) and *B. cinerea* on agar (Dowding & Royle 1971) seem to have low efficiencies as far as turning substrate N and P into sporophore or spore N and P are concerned (Table 7.8). If the sporophores of *A. bisporus* had been allowed to age until spore production ceased and the spores had been trapped, the utilization might have been higher. It is remarkable that two very different fungi have a similar range of efficiencies.

The reproductive allocation of unicellular organisms, is of course identical to their vegetative allocation so long as the cell numbers are still increasing. These organisms do not have to invest capital in an exploitative

Table 7.8. The efficiencies of utilization (%) of nutrients in the medium in the production of sporophores by *A. bisporus* (on compost) and of conidia by *B. cinerea* (on agar media).

Nutrient status	*A. bisporus*		*B. cinerea*	
	N	P	N	P
Non limiting	15	8	11·2	5
N—limited	21	6	8·0	1·5
P—limited	12	10	3·3	4
N+P limited	—	—	5·6	4

transport network, and at the same time cannot capitalize on solid plant remains, as they cannot penetrate plant cell walls. Some unicellular organisms do manage to exploit solid substrates with the aid of animals to break open new surfaces, e.g. maggots in carrion (Dowding 1967), or bark beetle larvae in wood (Leach 1940).

Discussion

So far there is information on changes in carbon and nutrient contents of complex solid substrates inextricably infested with micro-organisms. The allocation by these organisms to reproductive structures appearing outside the substrate can be measured, if they can be easily detached. Reliable estimates of the allocation to vegetative growth, in solid substrates, either in pure culture or in competition are more difficult to obtain. Organisms which can 'stretch' their reserves furthest are obviously in a position to gain new resources from a greater volume of substrate than are organisms (such as *Penicillium*) which cannot allocate their nutrients this way. The inability to 'recycle' protoplast to growing tips and to translocate nutrients over considerable distances may both be additional features of primary sugar saprophytes (sensu Garrett 1956).

There are several possible solutions to these complex problems. All are necessarily incomplete, but, after the observational phase of investigation some more definite questions (hypotheses) need to be answered:

(a) 'During vegetative growth of wood rotting fungi nutrients taken up by the mycelium are translocated to the growing tips:'

Analyses of uncolonized, just colonized (ca 2–3 days) and long colonized wood, will show whether nutrient concentration on a **volume** basis changes with zone. It is to be expected that gravimetric concentration will increase as the carbohydrates are in part lost as CO_2 (Fig. 7.4) during decay.

(b) 'Extraction of substrate nutrients into fruit body and spores is never complete:'

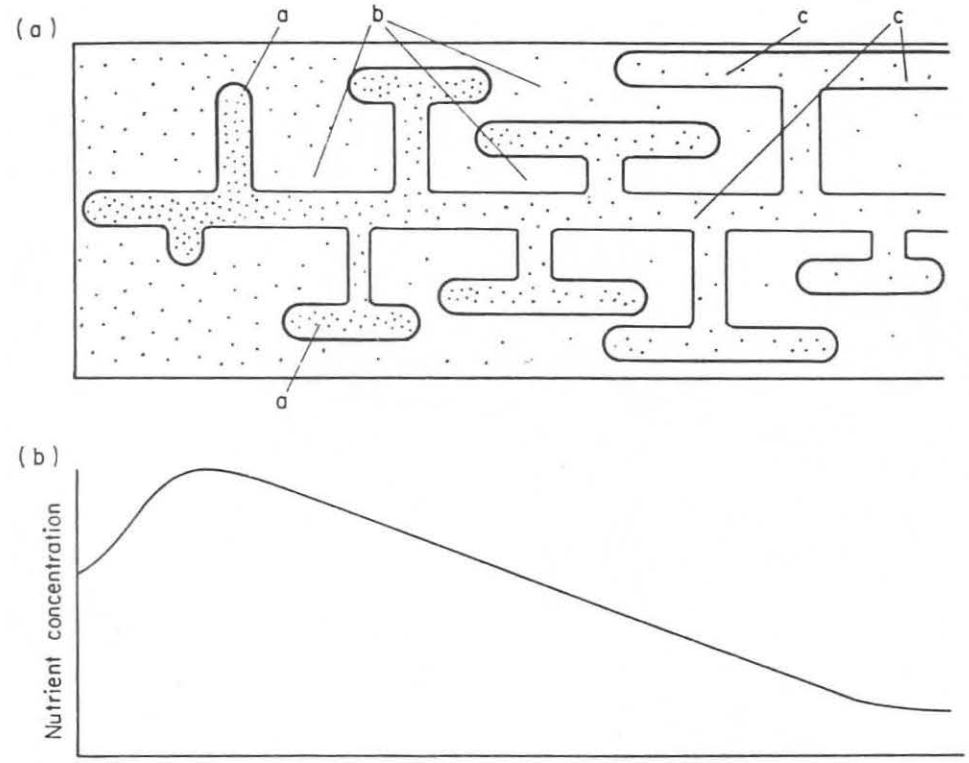

Figure 7.4. (a) Vegetative exploitation of solid substrate by a fungus showing:
a concentration of nutrients in the growing tips of hyphae, primarily in the advancing margin.
b absorption of substrate nutrients by the fungus.
c mobilization of nutrients within the fungus from older areas to the younger margin.
(b) The probable changes in nutrient concentration observed across the advancing margin of the colony shown in a.

Analysis of wood after fruit bodies have been matured (Hungate 1940) as well as during decay and before colonization will yield indices of extraction efficiency (e.g. Merrill & Cowling 1966). Cross-checks can be made by estimating the nutrients in the sporophore and in spores, if the production rate of spores is known.

(c) 'Competition lowers the extraction efficiency of individual species, but leads to more complete extraction of the whole:'

Herbivore dung appears to be the best substrate as the successions are well defined, as are the boundaries of the substrate. In addition there are sufficient nutrients for the production of basidiomycete fruit bodies. The hypothesis is supported by Webster's (1970) observation that the fruiting period of each component is shortened by competition, but not by Garrett's (1956) general hypothesis of nutrient limitation as one of the chief regulators of succession.

Nutrient loss from the substrate to fruit bodies could be estimated by either or both 'cropped' substrate and fruit body analysis. Pure cultures of components on sterilized dung would yield information on maximum extractive efficiency of each species, and of the rate of depletion.

Wood would also be a suitable substrate, but the units would have to be larger, necessitating subsampling. The size of unit would also be rather arbitrary and the time course of events much longer than on dung.

(d) '"Grazing" (by microfauna) (a) keeps the vegetative mycelium in an active state, (b) leads to a more rapid mobilization of nutrients and (c) slows decay (carbon removal) by fungi:'

These are all examples of effects the arthropod consumption of external fungal structures (usually fruit bodies) is supposed to have. The last is incompatible with the more widely held idea that microbial activity removes dry matter and possibly unpalatable compounds from freshly-dead material until it becomes palatable to the microfauna.

Simulation of grazing can be obtained by physical removal of external hyphae and fruiting structures. Depletion of nutrients and loss in dry weight of 'grazed' are then directly comparable with 'ungrazed' substrates.

More carefully controlled substrates can be built on an alpha-cellulose base. Known concentrations of more soluble carbohydrates and of mineral nutrient sources can easily be incorporated with reliable reproducibility. Hot alkali treatment removes fungal carbohydrates and leaves alpha-cellulose largely intact (Table 7.9). At early stages of growth, however, weight gains of fungal material are larger than 'gross decay', and likely that either (i) the inoculum is exerting a sizeable effect or, (ii) enzymic activity has resulted in some short chain carbohydrates in the substrate which are soluble in hot alkali or, (iii) are caused by the rapid accretion of nutrients (10 mgN and 2·5 mg P per flask).

Table 7.9. Weight loss of filter papers infected with *Chaetomium globosum* Kuntze ex Fries, hydrolyzed with 23M KOH.

Age of culture	?	?	?
Net~~t~~ weight change due to fungal activity (orig. wt. 300 mg)	+10	−26	−100
Subsequent weight loss on hydrolysis (e.g. fungal mycelium + non cellulose)	−16	−66	−104
Gross change (cellulose removal)	−6	−94	−204

After four weeks the metabolic efficiency (weight gain/carbohydrate consumed) drops from 66% to 50%. The latter figure is more in line with published data (Burnett 1969).

Nitrogen and phosphorus analyses will yield data on the rate and extent of uptake of these two nutrients after the (original) soluble component has been washed out.

Insoluble sources N and P can be localized at particular spots on a cellulose matrix, and export from them traced by ordinary analysis, or by the use of radio tracers (cf. Watkinson 1971, for work with P_{32} in agar cultures). This type of system can be used to test the same hypothesis as was tested by analysis of wood before and during decay, only in a more controlled fashion.

The extent to which microbial decay of natural substrates is accompanied by the synthesis of e.g. essential amino acids (Weller *et al.* 1958) (Table 7.10) may be as important for subsequent microfaunal activity, as loss in dry weight or removal of unpalatable compounds. Techniques for amino acid analysis are now routine, but are confined to the nutritional/biochemical fields of study. Investigators concerned with the flow of nutrients through the soil biota may well gain some insight to the parts played by various

Table 7.10. Proportions (%) of food protein intake in various fractions in the rumen of sheep (Weller *et al.* 1958).

In bacteria or protozoa	63–83
In plant residue	10–27
As soluble N	5–10

Table 7.11. Weight of mycelium and weight loss of cellulose substrate after 6 weeks' growth of *C. globosum* at 2 levels of N and P (mg. dw).

Nutrient status		Weight mycelium	Cellulose removed
C/N 17	C/P 68	104	204
C/N 17	C/P 680	60	80
C/N 170	C/P 68	16	33
C/N 170	C/P 680	17	33

Table 7.12. Fungal taxa growing as well on sodium phytate as on K_2HPO_4

Alternaria
Aspergillus niger
Botrytis cinerea
Botryodiplodia
Chaetomium globosum
Epicoccum purpurascens
Fusarium oxysporum
Trichoderma spp.
Stemphylium
Agaricus bisporus (Watson 1974)
Aspergillus spp. (Casida 1959)

groups of organisms by the use of methods at present confined largely to dietary analyses of food for farm animals. Similarly, plant nutritionists are paying increasing attention to phosphate as a limiting mineral in ecosystems. It has already been demonstrated that phosphate status can have a profound influence on the nitrogen uptake and growth of fungi (Dowding & Royle 1971; Watson 1974) (Table 7.11). Weller *et al.* (1958) note that phytic acid restricts phosphorus uptake by the sheep and that microbial transformation could have a considerable effect on the type of phosphorus compounds entering the intestine. A wide range of fungi can utilize sodium phytate as sole phosphorus source (Table 7.12) and may, therefore, not only move phosphorus outside the substrate, but also present it to the microfauna in a more digestible form.

References

BAUMBERGER R. (1935) A nutritional study of insects with special reference to micro-organisms and their substrate. *J. exp. Zool.* **28**, 1–81.

BHARGAVE S. (1972) Cellulolysis of filter paper and wheat straw by foot rot fungi. *Trans. Br. mycol. Soc.* **58**, 348–50.

BURNETT J.H. (1969) *Fundamentals of Mycology*. Arnold, London.

CHALAL D.S. & GRAY W.D. (1968) The growth of selected cellulolytic fungi on wood pulp. In: *Biodeterioration of Materials*, eds A.H. Walters & J.J. Elphick, Elsevier, Amsterdam. pp. 584–93.

CHANG Y. & HUDSON H.J. (1967) The fungi of wheat straw compost I. Ecological studies. *Trans. Br. mycol. Soc.* **50**, 667–77.

CHESTERS C.G.C. (1950) On the succession of microfungi associated with the decay of logs and branches. *Trans. Lincolnshire Naturalists Union* **12**, 129–35.

COCHRANE V.W. (1958) *The physiology of fungi*. J. Wiley, New York.

DOWDING P. (1973) Effects of felling time and insecticide treatment on the inter-relationships of fungi and arthropods in pine logs. *Oikos* **24**, 422–9.

DOWDING P. (1974) Nutrient losses from litter on IBP Tundra sites. In: *Soil organisms and Decomposition in Tundra*, eds A.J. Holding, O.W. Heal, S.F.Jr. Maclean and P.W. Flanagan, Tundra Biome Steering Committee, Stockholm.

DOWDING P. & ROYLE M.C.I. (1971) The uptake and partitioning of nitrate and phosphate by cultures of *Botrytis cinerea*. *Trans. Br. mycol. Soc.* **59**, 193–208.

DOWDING V.M. (1967) The function and ecological significance of the pharyngeal ridges occurring in some cyclorhaphous Diptera. *Parasitology* **57**, 371–88.

FRANKE-GROSSMANN H. (1963) Some new aspects in forest entomology. *Ann. Rev. Ent.* **8**, 415–66.

GARRETT S.D. (1956) *The biology of root infecting fungi*. Cambridge University Press.

GARRETT S.D. (1962) Decomposition of cellulose in soil by Rhizoctonia solani Kuhn. *Trans. Br. mycol. Soc.* **45**, 115–20.

GOTZ J.R., LIKENS G.E. & BORMANN F.M. (1973) Nutrient release from decomposing leaf and branch litter in the Hubbard Brook Forest, New Hampshire. *Ecol. Monog.* **43**, 173–91.

HAWKER L.E. (1951) *The physiology of fungi*. Methuen, London.

HUDSON J.H. (1968) The ecology of fungi on plant remains above the soil. *New Phytologist* **67**, 837–74.

HUNGATE R.E. (1940) The nitrogen content of sound and decayed coniferous wood and its relation to loss in weight during decay. *Botanical Gazette* **102**, 382–92.

KENDRICK W.B. & BURGES A.A. (1962) Biological aspects of the decay of *Pinus sylvestris* leaf litter. *Nova Hedwigia* **4**, 313–42.

LEACH J.G. (1940) *The insect transmission of plant disease.* McGraw-Hill, New York.

LEACH R. & MOORE K.G. (1966) Sporulation of *Botrytis fabae* on agar cultures. *Trans. Br. mycol. Soc.* **49**, 593–601.

LEVI M.P. & COWLING E.B. (1968) The effect of C/N ratio of the substrate on the growth, composition, cellulose production and wood destroying capacity of *Polystictus versicolor.* In: *Biodeterioration of Materials*, eds J.H. Walter & J.J. Elphick, Elsevier, Amsterdam. pp. 573–83.

MERRILL W. & COWLING E.B. (1966) The role of nitrogen in wood deterioration. Amount and distribution of nitrogen in fungi. *Phytopathology* **56**, 1083–90.

PIERIS G. (1947) *The Botrytis disease of Gladiolus together with a physiological study of certain Botrytis species.* Ph.D. Thesis, University of London.

PRESCOTT S.C. & DUNN R.G. (1959) *Industrial Microbiology*, 3rd edn. McGraw-Hill, New York.

RODIN L.E. & BASILEVITCH N.I. (1967) *Production and Mineral cycling in terrestrial vegetation.* Oliver & Boyd, Edinburgh.

SALISBURY E.J. (1942) *The reproductive capacity of flowering plants.* G. Bell & Sons, London.

TRESCHOW C. (1944) Nutrition of the cultivated mushroom. *Dansk Botanisk Arkiv* **11**, (6), 1–180.

WATKINSON S.C. (1971) Phosphorus translocation in stranded and unstranded mycelium of *Serpula lachrymans. Trans. Br. mycol. Soc.* **57**, 535–9.

WATSON J.M. (1974) *The nitrogen and phosphorus nutrition of* Agaricus bisporus. M.Sc. Thesis, University of Dublin.

WEBSTER J. (1970) Coprophilous fungi. *Trans. Br. mycol. Soc.* **54**, 161–80.

WELLER R.A., GRAY F.J. & PILGRIM A.F. (1958) The conversion of plant nitrogen into microbial Nitrogen in the rumen of the sheep. *Br. J. Nutr.* **12**, 421–9.

WOOD R.K.S. (1964) *Physiological plant pathology.* Blackwell Scientific Publications, Oxford.